ISSUES, IDEAS AND INFORMATION FOR PSYCHOLOGY STUDENTS

NO.8 - EVOLUTION

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1. HUMANS VERSUS CHIMPANZEES: GENETICS

1.1. GENETIC DIFFERENCES

Of the "three billion letters that make up the human genome, only fifteen million of them - less than 1 per cent - have changed in the six million years or so since the human and chimp lineages diverged" (Pollard 2009 p44). But in that 1% of difference are the basis of the gulf between humans and chimpanzees. It is now accepted that it is not big differences in the number of genes that matter, but rapid changes at key sites on the genome (Pollard 2009).

The mapping of the human genome in 2001 (International Human Genome Sequencing Consortium 2001) and the chimpanzee genome in 2005 (Chimpanzee Sequencing and Analysis Consortium 2005) has allowed the detailed comparison of the two. Areas that have changed can be harmless mutations or evidence of positive evolutionary selection.

Pollard (2009) reported finding, in 2004, a rapidly evolving sequence of 118 bases which became known as "human accelerated region 1" (HAR1) [1] [2].

HAR1 is found to be active in the brain, and, in particular, in neurons in the developing cerebral cortex. A malfunction in these neurons produces a disorder called lissencephaly, where the surface of the cortex is smooth (as opposed to the normally folded or wrinkled surface).

Another gene that is different between chimpanzees and humans is the FOXP2 gene. Mutations in this gene in humans means that individuals are unable to make the high-speed facial movements needed for speech despite having no cognitive deficits (Pollard 2009).

The modern version of the FOXP2 gene has been extracted from fossils of Homo neanderthalensis, which

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[1] There are now 201 other HARs discovered, of which many of them relate to brain development (Pollard 2009). While HAR2 (also known as HACNS1), for example, is linked to wrist and thumb development.

[2] Eighteen differences in this area between chimpanzees and humans (common ancestor - six million years ago), while there are only two differences between chimpanzees and chickens here (common ancestor - 300 million years ago)(Pollard 2009).

could suggest they had language (Pollard 2009).

Large brain size in humans is being linked to a gene called ASPM, where mutations in humans produce microcephaly (small brain size)(Pollard 2009).

Other gene differences relate to physiological changes between humans and chimpanzees, like AMY1, which produces enzymes involved in starch digestion (Pollard 2009). One explanation for the evolution of the "big brain" is satisfaction of its vast energy needs through increased starch intake.

Perry et al (2007) reported that high starch-eating populations today, like European Americans and Japanese have more copies of the AMY1 gene that low starch-eating populations, like Biaka (Central African Republic) and Mbuti (Democratic Republic of Congo)(both rainforest hunter-gatherers). Less copies of the gene were found in wild-born chimpanzees (Pan troglodytes) and bonobos (Pan paniscus). The authors felt that analysis of the AMY1 gene showed the importance of starchy foods in human evolution.

1.2. REFERENCES

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1.3. APPENDIX: BASIC GENETICS

1.3.1. The Cell

Each cell in the body contains a complete set of chromosomes. The chromosomes are numbered 1 to 22 in humans based on decreasing size. Chromosomes are spread in two ways.

The first process of cell division is known as mitosis. The new cell contains the exact duplication of pairs of chromosomes as the original.

While in the process of meiosis, the gametes (matured sex cells; ie: sperm or egg) receive half the pair of chromosomes of the parent. Thus during reproduction the pair of chromosomes are reformed from the mother and father's gametes.

However, one chromosome does not follow these rules

- the X chromosome. This chromosome can have two forms: XX (which determines a female) or XY (for male).

The chromosome complement is known as a karotype, which for humans is 46: 22 pairs (known as autosomes) the same for either sex and then XX or XY.

On occasions, there can be extra copies of a chromosome (known as trisomy) eg: Downs syndrome, and trisomy 21 (an extra copy of chromosome 21). Other chromosomal abnormalities include deletions or duplications of part of a chromosome.

1.3.2. Chromosomes

Chromosomes are made up of genes, which are based on DNA (deoxyribonucleic acid). DNA is made up of four bases: adenine (A), guanine (G), cytosine (C), and thymine (T). These are ordered around two chains wrapped together as the double helix.

The nature of DNA is such that A always pairs with T, and C and G. The sequence of bases is the genetic information.

Genetic information is transported within the cell by messenger ribonucleic acid (mRNA). Each molecule of mRNA contains a molecule of DNA (this process is transcription), and mRNA is translated into proteins. The proteins are, for example, leucine, glycine, and arginine. These are, simplistically, the building blocks for the physical manifestation of the gene's instructions.

1.3.3. Inheritance

Changes in the sequence of bases leads to changes in cell development. Point mutation is the substitution of one base for another, and is the most obvious example. Others include deletions (loss of sequence of bases), insertions (gaining of a piece of DNA), frameshift mutations (the loss of one base affecting the coding of others), and translocations (the breaking of part of a chromosome and reforming at a different site on a different chromosome) (figure 1.1). These changes can be advantageous in the evolutionary sense as well as disadvantageous.

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NORMAL SEQUENCE          ACCGTTTTA
DELETION                 ACCGTTT..
POINT MUTATION           ACCGATTTA
INSERTION                ACCTTGTTG
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Figure 1.1 - Examples of changes in sequence of bases.

2. HOW UNIQUE ARE HUMANS AND LANGUAGE?

2.1. HUMAN UNIQUENESS

The chimpanzee genome is 98.77% identical in terms of base-pairs of DNA to humans, while rhesus macaques and vervet monkeys only vary from humans by 5 to 7.5% respectively (Langley 2006).

"We humans are not as special as we might like to think. Over the past decade, hard scientific fact has steadily chipped away at our supposedly unique qualities, revealing many of them to be just more sophisticated versions of traits found elsewhere in the animal world" (Kenneally 2008).

Chimpanzees (Pan troglodytes) are now viewed as similar to humans in the following areas (Langley 2006):

* Emotional capacities;
* Affectionate family bonds;
* Long-term social relationships;
* Conscious awareness of self as separate from others;
* Altruism;
* Group aggression;
* Communication;
* Observational learning;
* Tool use;
* Understanding abstract symbols;
* Manipulating social situations for own purposes.

Tool-making as a unique ability to humans was emphasised by Oakley (1949) with the idea that bipedalism and manual dexterity allowed tool use which aided the development of intelligence and so on in each generation. Tool use, however, has been observed in non-human primates since then (eg: Goodall 1964; chimpanzees).

Moura and Lee (2004) reported tool use in the wild by capuchins in the Brazilian forest. This included using stones to dig out tubers and crack seeds.

Capuchin monkeys are now seen as having the highest "encephalisation quotient" (ratio of brain mass to body mass)(Langley 2006).

Tool use is taken as a characteristic of understanding cause and effect. For example, captive gorillas (Gorilla gorilla) and orang-utans (Pongo pygmaeus) use objects to retrieve out-of-reach food (Mulcahy et al 2005).

The ability to remember information is showed in varying degrees by most species, but being aware of what you can remember is more complex. This is known as meta-memory. Hampton (2001) showed that rhesus monkeys (Macaca mulatta) had such ability because they could decline to undertake a memory test which they knew they would fail.

Both "war" and "peace" have been observed with fights between neighbouring troops of chimpanzees, and reconciliation gestures after individual conflict (de Waal 2005).

"Humanity's special place in the cosmos is one of abandoned claims and moving goalposts" (de Waal 2005 p56).

Table 2.1 summarises the abilities unique and not unique to humans (Kenneally 2008) [3].

ABILITIES THOUGHT TO BE UNIQUE IN HUMANS BUT FOUND IN OTHER	ABILITIES THAT SEEM TO BE UNIQUE TO HUMANS
• Culture • Theory of mind • Emotions • Tool use • Morality	• Representational drawing (art) • Cooking food • Religious beliefs • Humour • Sport

Table 2.1 - Abilities unique and not unique to humans.

2.2. LANGUAGE

Pika et al (2005) observed that "Human communication is unique in the animal kingdom in any number of ways. Most importantly, of course, human communication depends crucially on linguistic symbols, which, to our knowledge, are not used by any other species in their natural

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[3] See http://www.newscientist.com/uniquelyhuman.

environment" (p41).

The use of different alarm calls is not the same as language which is individually learned and is "used to direct the attentional and mental states of others to outside entities referentially" (Pika et al 2005 p41). There is an inflexibility in the calls of many species as shown by infants reared in social isolation or with other species producing the basic calls (Pika et al 2005).

The focus of the debate on unique abilities among humans has become language. However, the capacity for language is not so unique if language is seen as "a suite of abilities" (Kenneally 2008). Many of these abilities have been reported in non-human primates.

2.2.1. Gesture Use in Communication

Gestures are used in communication by many monkeys and apes. But humans use gestures in ways similar to language, which is different to gesture use among non-human primates. Gestures, like pointing, can be instrumental (eg: "give me that") or referential (eg: "look at that")(Povinelli et al 2003). The latter seems only to be found in humans.

The way that non-human primates learn gestures is different to humans. It is not from imitation of others, but through a process of "ontogenetic ritualisation" (Tomasello 1996). Pika et al (2005) described the this process during social interaction:

> - Individual A performs behaviour X;
> - Individual B reacts consistently with behaviour Y;
> - Subsequently B anticipates A's performance of X, on the basis of its initial step, by performing Y; and
> - Subsequently, A anticipates B's anticipation and produces the initial step in a ritualized form (waiting for a response) *in order to* elicit Y (pp42-43).

For example, human infants raise their arms when wanting to be picked up. This is ritualised from the picking up process not learned by imitating other infants. "The main point in ritualisation is that a behaviour that was not at first a communicative signal becomes one by virtue of the anticipations of the interactants over time" (Pika et al 2005 p44).
This ritualised process explains one of the two types of intentional gestures used by chimpanzees - "incipient actions", like "arm-raise" to signal rough and tumble play which developed from raising the arm to hit the other. The other type are "attractors" (or attention-

getters)(eg: poking other animal)(Pika et al 2005).

Pika et al (2005) argued that even though non-human primates do not use gestures in the same way as humans, "because many of their gestures — in contrast to their vocalizations — are clearly learned and used quite flexibly, with adjustments for the attentional state of the recipient, it would seem plausible that the gestural modality of our nearest primate relatives was the modality within which symbolic communication first evolved" (p52).

2.2.1.1. Laboratory Experiments on Gesture Use

Studies of gestures among primates have been performed as laboratory experiments rather than as naturalistic observation.

Cartmill and Byrne (2007) showed that orang-utans will modify their gestures if they are misunderstood. Three adult female Bornean orang-utans (Pongo pygmaeus) and three adult female Sumatran orang-utans (Pongo abelii) from two captive populations in the UK were tested.

A desirable food, like bananas or bread, were placed on one dish in front of the orang-utan, but out of reach. An undesirable food (eg: leek, celery) was on another dish. The experimenter could give the orang-utan either the desirable food (whole goal condition), half the desirable food (part goal condition) or the undesirable food (non-goal condition). The experiment was repeated measures, and all behaviour of the animals was video-recorded.

At the start of the experiment, the experimenter waited silently for the orang-utan to gesture towards the desirable food. Each condition focused on the understanding of the communication by the experimenter - whole goal condition meant that the orang-utan's gestures were understood, while the non-goal condition was a failure to understand, and part goal was partial understanding. How the orang-utan behaved after receiving the food was recorded for sixty seconds. Did they continue to communicate in the non-goal and part goal conditions where the gestures had been misunderstood (table 2.2)?

In the whole goal condition, the orang-utan stopped gesturing as soon as the desirable food was given. This was expected because the gestures had successfully communicated their desire/goal. In the other two conditions the animals continued to gesture after the food given by the experimenter. In the part goal condition, gestures were repeated.

The orang-utans changed their gestures rather than

repeated them in the non-goal condition showing that the animals understood the original gestures had failed to communicate. "The difference in the tendency to repeat gestures shows that orang-utans are able to evaluate their own level of success in communication and modify their subsequent attempts accordingly. If they perceive their prior efforts as having partially succeeded, the orang-utans in our study repeat signals up to half the time. In contrast, if they have completely failed, they avoid repetition" (Cartmill and Byrne 2007 p1346).

CONDITION:	Whole Goal	Partial Goal	Non-Goal
Pre-delivery of food	Orang-utan gestures by reaching for desirable food,	Orang-utan gestures by reaching for desirable food,	Orang-utan gestures by reaching for desirable food,
Experimenter response	Give desirable food	Give piece of desirable food	Give undesirable
Post-delivery gestures	None	Repetition of gestures (60%); some new ones	New gestures (90%); few repetitions
Reason	Goal of communication achieved	Communication partly understood, so repetition of signals to gain rest of	Gestures originally misunderstood, so adjust with new gestures

Table 2.2 - Three conditions in the experiment by Cartmill and Byrne (2007).

The authors concluded that:

The strategy employed by the orang-utans resembles that of the parlour game charades, in which players try to get their team to guess the name of a book or movie by acting it out nonverbally. As a player gesticulates on stage, the team calls out their guesses as to what is being portrayed. If your team is close to your answer, the best strategy is to repeat and refine the signals that have already partially worked. But if your team completely misunderstands your gestures, it is better to switch to new signals until they guess something close to your goal. This strategy not only maximizes a player's efficiency in choosing an effective indicator, but also communicates to the team how close they are to understanding the intended meaning. Although the communication sequences of the orang-utans are perhaps not as sophisticated, they nonetheless

accomplish the same objectives (Cartmill and Byrne 2007 p1347).

Povinelli et al (2003) used seven chimpanzees housed at the University of Louisiana's LaFayette New Iberia Research Centre in their experiments. The basic experiment involved an individual chimpanzee on one side of a Plexiglas partition, and food (desirable object) and a distracter (undesirable object) on the other side.

Initially, the chimpanzees could reach through a hole in the partition for the object they wanted. Then the objects were placed out of reach of the chimpanzee, and could only be handed over by the human experimenter. In some cases, the experimenter deliberately looked away to see if the chimpanzee would gesture towards the food. "The results reveal that the chimpanzees noticed and altered their gesturing pattern when their partner's attention was not directed at the object that they themselves wanted" (p75).

2.2.2. Babbling

A process similar to the practising of different sounds before concentrating upon those of the natural language by young human babies has been recorded in young dolphins and monkeys. McCowan et al (2002) analysed communication data from adult and pre-adult bottle neck dolphins (Tursiops truncatus) and squirrel monkeys (Saimiri sciureus) as individual units of sound. The young of both species used wider repertoires of sounds (dolphins - whistles; monkeys - "chuck call") than the adults which suggested they were practising the sounds. Such behaviour can be compared to babbling in human babies.

2.2.3. Meaning to Specific Sounds

This has been noted in various species including "signature whistles" ("names") of dolphins, thirty-four different social sounds among humpback whales, and different cries among chimpanzees.

Animals change their rate of calling based on quality of food (eg: domestic chickens; Marler et al 1986). While monkeys, like cottontop tamarins (Saguinus oedipus), vary their calls for preferred food, independent of quantity (Elowson et al 1991). But language is more sophisticated than that. Calls as semantic labels would mean different sounds for different items by the caller and understood by the listener.

Humpback whales (Megaptera novaeangliae) produce "songs" (only males and related to breeding), and "social vocalisations" (both sexes). Dunlop et al (2007) acoustically categorised the latter sounds among

migrating whales over three years off the coast of
Queensland, Australia using hydrophone buoys in a ten-
kilometre study area. 660 social vocalisations from
sixty-one pods were analysed, and classified as thirty-
four separate types (27 were heard from more than one
group)(table 2.3).

CATEGORY OF SOUNDS	INDIVIDUAL TYPES OF SOUNDS
Low frequency (5)	wops, thwops, snorts, grumbles, signs
Mid-frequency harmonic (11)	sirens, short moans, horns, violins, groans, ascending moans, modulated moans, cries,
High-frequency	ascending shrieks, descending shrieks, squeaks
Amplitude-	growls, purrs, trills
Broadband, "noisy", and	blows, barks, bellows, creaks, screeches, scream
Repetitive (6)	grunts, croaks, yaps, yelps, pulses, low yap

Table 2.3 - Thirty-four social vocalisations made by
humpback whales.

        The researchers have described the different
vocalisations, and admitted that further study is needed
to explain the purpose of the sounds. This will include
the question of whether these sounds constitute a
language.

        2.2.3.1. Chimpanzees

        There has been a lot of interest in the chimpanzee
pant hoot sound. "Part of the significance of the search
for context-specific pant hoot variants in chimpanzees,
then, lies in exploring potential evolutionary precursors
to the referential, or semantic, qualities of human
language. Their very close phylogenetic affinity to
humans by itself recommends chimpanzees as especially
promising candidates for language precursors" (Notman and
Rendall 2005 p178).
        For calls to be seen as language they must be
"functionally referential". This means that the call
varies with the "production context", and with receivers
present (Notman and Rendall 2005).
        Are chimpanzee pant hoot sounds "functionally
referential"? Different studies have concluded different
functions for these calls:

- To announce food found and location of it (Wrangham 1977);
- To advertise the social status of the caller and to attract mates (Clark and Wrangham 1994);
- To maintain cohesion within the group and communicate with social allies (Mitani and Nishida 1993).

Notman and Rendall (2005) attempted to clarify the functions of pant hoots by recording wild chimpanzees (Pan troglodytes schwienfurthii) in the Bundongo Forest Reserve, Uganda. Each time an animal called, its behaviour was categorised into travelling, feeding, arriving at food, or resting, and the social circumstances were also noted (eg: caller alone; arrival of other chimpanzees after call).

Differences in the acoustic dimensions of the pant hoot were found depending on the behaviour being performed (eg: the climax elements varied for travelling), and the presence of others. Table 2.4 gives some examples of the acoustic differences in the pant hoot stages.

STAGE IN	ACOUSTIC DIFFERENCES
Build-up	Pitch: 230 Hz (resting on ground) vs 283 Hz (arriving
Climax	88 Hz (travelling on ground) vs 62 Hz (feeding); 68 Hz
Let-down	Varied depending on group size, but not food source

Table 2.4 - Acoustic differences in stages of pant hoots depending on situation.

It was also found that pant hoots among the seven chimpanzees studied were individually distinct such that the researchers could accurately tell who was calling (average: 87.4% of time).

Notman and Rendall felt that the purpose of the pant hoot was to signal identity (like a name) and to co-ordinate social activities and relationships. But they felt that the sounds were not "functionally referential": "We further suggest that the subtle structural differences observed in some contexts reflect the different effects on vocal production introduced by the variable arousal and motivation, physical demands, or vocal effort associated with calling in those contexts" (p187).

So chimpanzees vocalise when approaching food, and others appear to respond to the sounds. Slocombe and

Zuberbühler (2006) sort to establish if acoustically distinct "rough grunts" were linked to different foods among a captive population at Edinburgh zoo and a wild population of chimpanzees in the Budongo Forest Reserve, Uganda.

In the captive population, nine different foods were tested by offering pairs in an experimental procedure to four chimpanzees, while the wild population study was a naturalistic observation of responses to three foods by four adult males.

Acoustic differences in the calls were recorded for high, medium and low preference foods, and differences between the high preference foods themselves (bread, banana, mango) at Edinburgh zoo. The wild chimpanzees showed differences between levels of preferred food, but not between individual food types. So, in the highly limited environment of captivity, the chimpanzees appeared to be using grunts as semantic labels.

The ability to alter the nature of a call depending on the audience is another aspect of language here. Slocombe and Zuberbühler (2007) recorded the vocalisations of wild chimpanzees in the Budongo Forest, Uganda during conflicts, and, in particular, the victims of attacks. The screams were measured for duration, rate (number per second), and bout (total) length. Four levels of aggression were also recorded.

Acoustic analysis showed that the screams of victims were different depending on the level of aggression. The victim also changed their screams depending on the audience, particularly if it contained an individual of equal or higher rank than the aggressor. In some cases, the high-ranking individual in the audience responded to stop the aggression. The authors concluded that:

> Our data support the hypothesis that one function of chimpanzee screams is to recruit aid during conflict. Victims modified the acoustic structure of their calls to increase the chances of eliciting help from high-ranking individuals when they most needed it, that is, during severe cases of aggression. If high-ranking individuals were present, victims facing severe aggression gave longer, higher pitched screams, with peak energy later in the call, at a slower rate than when they were absent. These screams were acoustically consistent with screams given in cases of very severe aggression. This is despite the trend for the actual level of aggression to be less severe... when high-ranking individuals were in the audience. If faced with mild aggression, however, chimpanzees did not modify their calls in the same way (Slocombe and Zuberbühler 2007 p17232).

The exaggeration of the level of aggression by the

victim's scream is an example of "tactical deception". This is the ability to manipulate others for your own benefits. Slocombe and Zuberbühler noted that their "data provide evidence for this ability, and to our knowledge, this is the first systematic empirical evidence to show that nonhuman primates are able to exaggerate distress to manipulate other group members. Unfortunately, however, our study does not allow us to make conclusive statements about the mental processes that underlie this behaviour.." (p17232).

Language involves learning in the sense of adapting to local differences in the group. So a human who moves from one part of the country to another will learn the local or dialectic differences of the new area.
Some evidence of this learning to produce within-group similarity and between-group difference has been reported in the pant hoot structure of captive chimpanzees. Marshall et al (1999) compared male chimpanzees at two sites in the USA - Lion Country Safari, Florida, and North Carolina Zoological Park. Each group has members with diverse origins which rules out a genetic basis to the vocalisation differences.
The typical pant hoot by a male chimpanzee has four parts - introduction (one long sound), build-up (short inhaled and exhaled sounds getting faster and rising pitch), climax (scream), and let-down (similar to build-up)(Goodall 1986). Acoustic analysis of the pant hoots found significant differences between the two groups (table 2.5), while the overall length did not vary (approximately six seconds).
The researchers felt that the differences were due to learning. This was also seen in a variation of vocalisation ("Bronx cheer" - "raspberry-like sound") made by one male arriving at the Florida site. Soon after, six other males were making the sound.

	FLORIDA GROUP	NORTH CAROLINA GROUP
Pant hoots with		More (90% vs 11%)
Duration of		Longer (mean 2.4 vs
Build-up elements	More (mean 9.5 vs	
Build-up	Longer (mean 3.8 vs	
Climax		Longer (mean 1.9 vs

(After Marshall et al 1999)

Table 2.5 - Significant differences in pant-hoot structure between two groups of male chimpanzees.

2.2.3.2. "Words"

Differences in calls have been shown to distinguish predatory category, distance to predator and urgency to respond. Different calls for different predators would suggest that the prey animal had "a causal understanding of their predator's behaviour" (Griesser 2008).

Black-capped chickadees produce a "chick-a-dee" alarm call for terrestrial predators or a perched aerial predator (mobbing call), and a "seet" alarm call for flying predators (Templeton and Greene 2007). The calls also distinguish the size of the bird predator, as small raptors have greater manoeuvrability and are a greater risk. The calls vary subtly in rate as well as frequency (Templeton et al 2005). "Chickadees have one of the most sophisticated alarm call systems yet discovered and encode complex information in subtle variations within their calls" (Templeton and Greene 2007 p5481).

Griesser (2008) showed that Siberian jays (Perisoreus infaustus) distinguished in their calls between hawks sitting, searching or attacking.
Griesser studied a wild population of jays in northern Sweden. The different calls in relation to hawk behaviour were observed, and tested with a hawk model and a playback experiment. Acoustic analysis showed that different calls were used for a perched hawk (mobbing call), a hawk searching for prey (alert call), and an attack.
The playback experiment allowed the researcher to test the meaning of the call to the hearer. For example, a playback of an alert call caused the jays to fly to the nearest cover and freeze, which was the typical behaviour. A playback of the mobbing call cause the listeners to group together ready to mob (attack) the predator (table 2.6).

TYPE OF CALL	BEHAVIOUR IN RESPONSE TO PLAYBACK
Alert - hawk searching	Hide; freeze; passive predator search*
Attack	Hide; passive predator search*
Mobbing - hawk on perch	Mobbed hawk; active predator search**
Control - foraging call	Continued foraging

(* = scanning environment while hidden; ** = scanning environment in open)

Table 2.6 - Behaviour of Siberian jays in response to different calls in the playback experiment.

The playback experiment exposed twelve groups on

different days and in random order to the four different calls (3 calls for hawks and control call) for ninety seconds each. A speaker was concealed in a tree five metres from a feeder, and reactions were video-recorded during and for ninety seconds after the playback.

2.2.4. Syntax (Grammatical Rules)

"Syntactic rules allow a speaker to combine signals with existing meanings to create an infinite number of new meanings" (Zuberbühler 2002 p293). For example, marler (1972) described the call of Black-and-white colobus monkeys (Colobus guereza) which involved a roar and a "snort", and was involved in establishing territory. But the "snort" by itself was an alarm call.
Playback experiments with other apes and monkeys have used calls with normally and abnormally rearranged sounds, which the listener is able to distinguish (eg: gibbons; Hylobates agiles; Mitani and Marler 1989).

Zuberbühler (2002) investigated the calls of wild Campbell's monkeys (Cercopithecus campbelli) in the Tai Forest, Ivory Coast. They have a basic "eagle alarm call" and a basic "leopard alarm call" which can be modified by preceding low-pitched "booms". Zuberbühler played these different calls to 50 Diana monkey groups (Cercopithecus diana), which understood the Campbell's monkeys' calls, to see the reaction. There were eight conditions using male calls (table 2.7).

CONDITION	CALL USED
Baseline - leopard	Campbell's leopard alarm
Test - leopard	Booms and Campbell's leopard alarm
Baseline - eagle	Campbell's eagle alarm
Test - eagle	Booms and Campbell's eagle alarm
Control to baseline:	Diana leopard call
Control to test:	Booms and Diana leopard call
Control to baseline:	Diana eagle alarm
Control to test:	Booms and Diana eagle alarm

Table 2.7 - Eight conditions of playback experiment by Zuberbühler (2002).

Playback of the eagle and leopard alarm calls of the

Campbell's monkeys caused the Diana monkeys to produce their own versions of the calls and respond as if that predator was present. When "booms" preceded the alarm calls, the Diana monkeys did not respond (table 2.8).

TYPE OF CALL	MALE	FEMALE
Leopard	5	5
Booms - leopard	0	1
Eagle	5	3
Booms - eagle	0	0

(After Zuberbühler 2002)

Table 2.8 - Alarm call rate (calls/minute) by Diana monkeys on hearing Campbell's monkey calls.

It seems that the "boom" sounds had meaning in relation to the subsequent call. So, for example, an eagle alarm call meant an immediate danger of an eagle, while a boom followed by an eagle call meant a general disturbance not requiring immediate action. "It provides evidence.. that some calls can be combined according to structural rules to form more complex utterances, and that these combinations are linked with underlying changes in meaning" (Zuberbühler 2002 p298).

Zuberbühler compared the "boom" sound to "linguistic hedges" (Lakoff 1972), like "maybe", which when added to a sentence change the meaning. "Of course, this analogy is far from perfect, mainly because there is no evidence that the booms have comparable effects on the meaning of any other call, apart from the two alarm call types investigated" (Zuberbühler 2002 p297).

The ability to distinguish the alarm calls of another species was also tested for red-breasted nuthatches (Sitta canadensis) hearing the calls of Black-capped chickadees (Poecile atricopillus). Templeton and Greene (2007) played calls in response to a great horned owl (Bubo virginianus)(large predator; low threat), a northern pygmy owl (Glaucidium gnorma)(small predator; high threat), and a house sparrow (Passer domesticus)(control; no threat). The calls were mobbing calls towards the predator, and it was expected that the listener would approach the playback speaker.

There was a significant difference in the response of nuthatches to the calls in terms of approaching the speaker - 92% of trials for small predator call, 69% for large predator call, and 23% for control. Other behaviours were observed in response to the calls (table 2.9).

	LARGE PREDATOR	SMALL PREDATOR	CONTROL CALL
Wing-flick display (sign of agitation)	35	79	0
Vocalisation	65	91	25
Mean time mobbing	83	210	0

Table 2.9 - Black-capped chickadee calls that elicited behaviours from red-breasted nuthatches.

This research showed that "nuthatches discriminate between subtle differences in chickadee alarm calls that contain information about the size of potential predators. The data in this study show that animals can make sophisticated anti-predator decisions from information contained in variations within a single type of heterospecific alarm call" (Templeton and Greene 2007 p5481).

2.2.4.1. Different Types of Syntax

But there are different types of syntax. "Finite state grammar" (FSG) follows the (AB)n rule - sound "A" followed by sound "B" (eg: AB, ABAB etc) and "phrase-structure grammar" (PSG) has the AnBn rule - a given number of "A" sounds followed by "B" sounds (eg: AABB, AAABBB)(Kenneally 2008).

Fitch and Hauser (2004) played sequences of sounds to cotton-top tamarin monkeys (Saguinus oedipus). They reacted with surprise to (AB)n violations, but not AnBn, whereas adult humans noted both.

Sequences of human speech sounds were tested using the familiarisation/discrimination paradigm (figure 2.1). This involved familiarising the animal to a sequence by playing it many times (60 sequences in 20 minutes) with food rewards, and then playing a sequence that violated the pattern. A surprise reaction, measured by the animal turning towards the playback speaker, was taken as noticing the violation in the sequence.

The monkeys were only exposed to one type of grammar (FSG or PSG). The tamarins noted the FSG violations with 72% of the ten monkeys looking towards the speaker when a violation occurred, but only 29% looked with violations of the PSG sequence (table 2.10). Undergraduates tested on the same sounds (with three minutes training) scored 92% and 85% correct respectively.

```
"A" syllables = ba, di, yo, tu, la, mi, no, wu
"B" syllables = pa, li, mo, nu, ka, bi, do, gu


FSG (ABAB)


Example = no-li-ba-pa
Violation = no-li-ba-di (ABAA)


PSG (AABB)


Example = yo-la-pa-do
Violation = yo-la-tu-do (AAAB)
```

Figure 2.1 - Examples of grammatical sequences similar to those used by Fitch and Hauser (2004).

	VIOLATIONS	NON-VIOLATIONS	SIGNIFICANCE
FSG (ABn)	72	34	p = <0.007
PSG (AnBn)	29	31	ns

Table 2.10 - Percentage of tamarins looking towards the playback speaker when a new grammatical sequence was played.

The tamarins appeared to understand the rules of FSG, but not PSG. This study is the third failure to show that these animals understand FSG and PSG [4].

However, Gentner et al (2006) found starlings noted both types of violations to natural starling sounds. The researchers used the basic motifs (acoustic units) of European starling (Sturnus vulgaris) song to create a "language". The motifs were whistles, warbles, rattles, and high-frequency sounds. A FSG example would be "rattle-warble-rattle-warble" (AB^2), and "rattle-rattle-warble-warble" (A^2B^2) would be an example of PSG. The eleven starlings were trained by operant conditioning to respond to the two types of grammatical sequence.
After training, new sequences were introduced based on the two types of grammar, and the birds were able to recognise them, compared to agrammatical sequences, at levels significantly above chance.

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[4] The other two studies are Hauser et al (2001, 2002).

2.2.5. Combination of Sounds

Male putty-nosed monkeys (Cercopithecus nictitans martini) combine sounds which communicate the caller's identity, threat type, and how the caller responding to the threat. Arnold and Zuberbühler (2006) investigated their calls in Gashaka Gumti National Park, Nigeria.

These monkeys have two main predators - eagles and leopards - which require different responses. The alarm calls were recorded in response to the playback of eagle shrieks and leopard growls.

Two call types, "hacks" (shorter) and "pyows" (higher frequency) were distinguished acoustically. The two sounds were combined in different ways for both predators (table 2.11), and the hack-pyow units seemed to follow certain rules.

TYPE OF PREDATOR	MONKEY CALLS
Leopard	Pyow only (52.9% of trials); pyow-hack (35.3%); pyow-hack-hack (11.8%); hack only
Eagle	Hack only (60% of trials); pyow-hack (30%);

Table 2.11 - Combination of sounds made by putty-nosed monkeys.

The researchers concluded that while "individual calls did not qualify as vehicles of semantic content, these males produced structurally unique call sequences that provided sufficient information for receivers to select appropriate anti-predator responses" (Arnold and Zuberbühler 2006 p643).

2.2.6. Conclusions

Functionally referential use of calls means that they have production specificity (relate to a particular event), are independent of context (ie: can be used in any situation where appropriate), and have separate structure/units that allows combination in some way (Evans 1997).

Whether language is unique to humans depends upon how much different animal calls fulfil these criteria. Table 2.12 summarises the studies reported here and the findings in relation to human language.

ABILITY	EXAMPLE OF RESEARCH
Young practice	Bottle neck dolphins and squirrel monkeys
Intention in	Orang-utan and chimpanzees adapt gestures if
Different calls for different things	Chimpanzees different pant hoots, especially for different foods in captive population; different alarm calls carrying information about type of predator and speed of response
Differences between groups ("social	Differences between captive populations of chimpanzees
Grammar	Some use of "grammar" by monkeys, and

Table 2.12 - Summary of abilities related to language in studies reported in this article.

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3. EVOLUTION OF INTELLIGENCE IN PRIMATES

3.1. INTRODUCTION

Byrne (2000) summarised the issues related to understanding evolution:

> To describe "the evolution" of any characteristic,
> morphological or behavioural, requires at least
> two contributions. Each contribution may be
> understood as an answer to the same question,
> "How did the characteristic evolve?," but neither
> provides a complete answer on its own. In the
> first place, we may inquire about the *historical*
> aspects: at what approximate date did the
> characteristic first evolve in the lineage under
> consideration, in what ancestral species, and
> before or after which other characteristics.
> All of these questions may be addressed without
> touching on the second contribution, the *causative*
> aspects: what environmental features so significantly
> favoured the new characteristic that natural selection
> perpetuated it in subsequent generations, and out
> of what original set of genetically encoded characters
> was it selected (p545).

When trying to understand the evolution of a particular characteristic or behaviour, species are grouped into clades (Hennig 1966) based on shared, derived characteristics that come from a common ancestor.

3.2. EVOLUTION OF PRIMATE INTELLIGENCE

In understanding the evolution of primate intelligence, Byrne (2000) distinguished between the primate ancestor, the simian ancestor, and the great ape ancestor (figure 3.1).

i) The primate ancestor - The common ancestor of all primates (50 million years ago) was "not likely to have been specialised for intelligence". This is assumed from the primate branch of strepsirhines today (eg: ring-tailed lemurs) who show little intellectual ability in laboratory experiments, like being slow to learn (Byrne 2000).

```
SPLITS                                    SPECIES TODAY

(1) PRIMATES      50 MYA

     STREPSIRHINES          →         Ring-tailed lemur

     SIMIANS


(2) SIMIANS 30 MYA

      NEW WORLD MONKEYS      →         Tamarin/Capuchin


(3) SIMIANS 25 MYA

      OLD WORLD MONKEYS      →         Baboons/Macaque

     GREAT APES


(4) GREAT APES    12 MYA

                             →         Orang-utans


(5) GREAT APES    6 MYA

                             →         Gorilla


(6) GREAT APES    4.5 MYA

                             →         Chimpanzees/Bonobos

                             →         Humans
```

MYA = million years ago

(1) Strepsirhines split away from other primates (called simians)
(2) New World monkeys split from other simians
(3) Old World monkeys split from other simians leaving great apes
(4) Orang-utans split from great apes
(5) Gorillas split from great apes
(6) Great apes divide into chimpanzees (and sub-divide later with bonobos) and humans

(After Byrne 2000)

Figure 3.1 - Key evolutionary splits in primates.

    ii) The simian ancestor - This common ancestor from
30 million years ago is believed to have a larger brain
relative to body size and showed signs of intelligence
based on the ability of rapid learning. "Early simians
were thus likely to have been quantitatively superior to
most other mammals, but not to show any qualitative
differences in cognition from them" (Byrne 2000 p551).

iii) The great ape ancestor - From 12 million years ago, this common ancestor of gorillas, orang-utans, chimpanzees, and humans would have been qualitatively different to other primates. For example, the simian ancestor may have used "tactical deception" achieved through very rapid learning, whereas the great ape ancestor had the ability from a "theory of mind" (Byrne 2000). Tactical deception can be seen in making a false alarm call which allowed the caller free access to food. The simian ancestor would learn this behaviour from experience, whereas the great ape ancestor has some "mind-reading" abilities. The theory of mind is the ability to understand how another individual thinks based on your own way of thinking. Thus, "I run away when I hear an alarm call, so they will run away when I make an alarm call".

There are key abilities that are taken as signs of intelligence including tactical deception, tool use, and learning novel and complex skills by observation and imitation. Such abilities would evolve because of selective pressures in the physical and social environment for complexity (Byrne 2000).

3.3. EVOLUTION OF HUMAN INTELLIGENCE

The complexity of the human mind compared to other species is not seen as due to single differences, but a product of a number of evolutionary pressures. The two main pressures discussed here are "social intelligence" and the problems faced by living on the savannah.

3.3.1. Social Intelligence

Whiten and Byrne (1997) proposed that human intelligence developed initially because of the social behaviour of early humans. The need for co-operation, or deceit and social manipulation. This is known as the "Machiavellian hypothesis".
Thus intelligence evolves as a means of solving problems in each species, and in humans, the main problems were linked to social interactions.

The key is the complex social order that early humans formed compared to other species. There are advantages to such groups in terms of sharing skills and resources, but there is also an individual advantage to exploiting other individuals within the group: competition and co-operation together. Such demands, and knowing when to use which one, requires a higher-level intelligence. Humphreys (1976) calls it a "creative intelligence".

Smith and Stevens (2002) summarise the state of early human societies:

> ..negotiating what is of best advantage to you
> at least cost, while the individual you are
> interacting with is making exactly the same
> calculations. Thus, co-operation becomes not
> a naive 'trusting' of others, but rather a
> calculated option. As an individual, the ability
> to cheat others would clearly increase one's
> chances of maximum individual benefit...the
> individual you are attempting to cheat will
> maximise his or her benefit by being able to
> predict when you are cheating. So begins a series
> of elaborate and complex calculations (p125).

The ability to survive in such a world will be enhanced by a "theory of mind": the ability to understand the intentions of another individual.

Whiten (1996) sees four forms of ability here:

i) Implicit mind-reading - to understand another's experiences from their actions; eg: laying down to sleep means experiencing tiredness;

ii) Counter-deception - to distinguish between the action and another intention; eg: laying down to make you think they are tired, and thus avoid talking to you;

iii) Recognition of intervening variables - knowing that events cause the person to behave in a particular way; eg: a loud noise will cause the person to run away;

iv) Experience projection - own experiences allow prediction of how person would behave in same situation.

To what degree, chimpanzees have these abilities is open to discussion, but the evolutionary basis is there.

3.3.2. "Modular Mind"

Social intelligence is one of the pressures upon the development of the human mind. Another pressure which could go hand in hand is related to the development of cognitive processes. For example, the ability to use social intelligence is further enhanced by a good memory and the ability to learn socially relevant information (Byrne 1999).

These developments can be seen in the technical skills of tool-use and imitation. Again there is some evidence of these abilities among chimpanzees, but the

key in humans is the level of these skills.

Whiten (1999) argues that the move from the forests to open savannah was crucial for early human evolution. Catching prey required very different cognitive abilities, which relied upon memory and learning, compared to ancestors in the forest.

But tool-use by itself would not be enough to lead to the evolution of the "big brain": especially the sudden increase in size about two million years ago. Tool use by Neanderthals and Homo erectus is little different to chimpanzees today (Byrne 1995).

Evidence to support the importance of the move to the savannah comes from observations of hunter-gatherers in the modern world; eg: !Kung San of Kalahari desert. They shoot the prey with poisoned arrows; the prey runs off; and later the hunters track the animal to find the dead corpse (Lee 1979).

This is very different to how other species catch prey by always maintaining visual contact with it. The !Kung San method of hunting uses many cognitive skills: planning, representation of objects not physically present, reasoning, and the ability to make "technology" (ie: arrows and bows)(Whiten 1999).

These skills develop in a social context. Furthermore, the evolution of language improves both social interaction and the planning and proceed of hunting.

The cognitive skills of sophisticated hunting and social intelligence would be examples of "functionally differentiated modules" or "domain-specific mental modules" (Cosmides and Tooby 1992) in the brain - each module having a specific function. The existence of these modules allows problem-solving, and, in particular, in new situations. The specifics change, but the general principles of the modules remain. For example, the module related to exchange allowed for barter in the past and detailed monetary transactions today (Gigerenzer 1997).

This module may involve certain abilities: including the recall of past exchanges with specific individuals, who cheats, and the knowledge of costs and benefits. The module may include cognitive, emotional, behavioural, and motivational processes (Gigerenzer 1997).

Cosmides and Tooby (1992) see the ability to detect cheaters as crucial. If "cheater-detection" is so important, then this ability will be evident in remembering information. Mealey et al (1996) have found this to be the case. Students were shown male facial photographs for a short period of time along with information about the person (in particular, whether they were trustworthy or not). One week later, recall was better for the faces described as untrustworthy.

Another key module is relational and abstract

thinking (Cosmides and Tooby 1987). The modules that exist today in the brain are those that gave evolutionary advantages to early humans. The idea of modules tends to be a theoretical framework rather than clear physiological regions of the brain.

Geary (1998) lists some of the potential modules: language; facial processing; detection of cheating; theory of mind; kin recognition; in-group recognition; out-group recognition; social ideologies; representation of objects.

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4. GROUP SELECTION TO EXPLAIN ALTRUISTIC BEHAVIOUR

4.1. INTRODUCTION

Evolutionary theory has found it difficult to explain altruistic and moral behaviour. If survival of the individual is paramount, then altruistic behaviour would be a disadvantage (ie: giving freely to another at own expense).

Darwin's (1871) explanation related to advantages for the group: "..a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe.. [but] an immense advantage to one tribe over another" (p166; quoted in Wilson and Wilson 2007). This is the idea of group selection (or now called "multi-level selection theory"; Wilson and Wilson 2007). The idea that "one mixed bag of individuals can be 'selected' as a group over other heterogeneous groups from the same species" (Mirsky 2009).

However, group selection was widely rejected in the 1960s for lack of evidence, and theoretical problems (Wilson and Wilson 2007).

"Naive group selectionism" is linked, for example, to Wynne-Edwards (1962) who saw animals evolving to regulate their population size and avoid overexploitation of resources. At a certain population size, individuals create a signal (an adjustment mechanism) that stops reproduction.

Groups where individuals reduce their reproduction rate when food is scarce, for example, will have a better chance of survival than groups where individuals strive for their own evolutionary success. The problem, however, is to explain such an underlying mechanism (Hayes 1994).

4.2. ALTRUISTIC BEHAVIOUR

The evolutionary explanation of altruism has been taken up primarily by kin selection/inclusive fitness, the "selfish gene"/extended phenotype, and evolutionary game theory/reciprocal altruism.

Hamilton (1964) proposed the theory of kin selection (or inclusive fitness) to explain altruistic behaviour

towards kin, like a mother dying to save her offspring.

Dawkins (1976; 1989) reduced all behaviour to the survival of the gene rather than the survival of the individual. He proposed the Central Theorem of Extended Phenotype: "An animal's behaviour tends to maximum survival of genes 'for' that behaviour, whether or not those genes happen to be in the body of the particular animal performing it" (Dawkins 1989 p253).

A mother who dies to save three offspring will have saved one and a half times her own genes because each offspring carries half of the mother's genes (3 x ½ = 1). Though the mother dies, for Dawkins, it is the genes that survive, and evolution is about the continuation of the genes not the individual (ie: "the survival of the fittest genes"). Altruism is, thus, based on the degree of "genetic overlap" between individuals.

Dawkins (1989) used this example to show the principles of his idea. An individual finds eight items of food, but can only eat three. If each item of food is worth +6, selfishness produces a benefit of +18 (3 x +6). For the benefit of the genes, the individual could eat two items only and call three other animals to eat the rest: a brother (sharing half the same genes), a cousin (sharing 1/8), and unrelated animal (zero shared genes). This behaviour would give a total score of +19 , which is calculated thus:

```
Individual        2 food items x +6    = 12
Brother           2 x +6 x 1/2         = 6
Cousin            2 x +6 x 1/8         = 1
Unrelated         2 x +6 x 0           = 0
                              Total    +19
```

For Dawkins, sharing, which appears as altruistic behaviour, is, in fact, beneficial to the individual's genes. If this is right, then animals should be altruistic towards closer kin than less related and non-related individuals.

Trivers (1971) proposed the idea of "delayed reciprocal altruism" to explain altruistic behaviour towards non-kin: "an exchange of altruistic acts between the same two individuals so that, in total, both obtain a net benefit". In other words, the idea of returning favours, or "tit-for-tat".

It is important that a relationship exists between the individuals involved, and there is an opportunity for a favour to be returned at a later date.

Game theory is a mathematical principle that has also been applied in biology to explain animal behaviour

(Maynard Smith 1974, 1982). A key concept is the evolutionary stable strategy (ESS), which is the strategy, if most members of a population adopt, that cannot be bettered. An individual's strategy will depend upon the population strategy.

So, for example, if an ESS is co-operation, then an individual strategy of selfishness could work in the short-term, but co-operation would be better in the long-term. On the other hand, an ESS of selfishness would make co-operation a bad idea for an individual. Mathematical models are designed using game theory, and they vary the costs and benefits of certain behaviours.

4.3. GROUP SELECTION

Group selection in the form of multi-level selection theory is making a return, as argued by Wilson and Wilson (2007). Evidence from populations of bacteria, for example, are showing that individuals "sacrifice" their own benefits for that of the group compared to another group.

Pseudomonas fluorescens bacteria suck oxygen out of a liquid and limit themselves to a thin habitable layer near the surface. Some individual bacterium produce a polymer that creates a floating mat for all the bacteria. If "freeloaders" (who do not produce the polymer) reproduce too much, the mat sinks and everybody dies. Groups containing a certain number of altruists (polymer producers) have a selective advantage over groups with no or few altruists (Rainey and Rainey 2003).

The current version of group selection accepts that evolution happens at different levels, hence the term, "multi-level". Selection is constantly "taking place on multiple levels simultaneously" (Mirsky 2009). While, overall, "Selfishness beats altruism within single groups. Altruistic groups beat selfish groups" (Wilson and Wilson 2007).

Table 4.1 compares the different "types" of evolution and altruism.

"TYPE" OF	FOCUS	COMMENT
Traditional/Darw	Individual	Altruists exploited by cheaters
Selfish gene	Individual gene	Altruism only makes sense for
Group selection	Group	Group as whole benefits from

Table 4.1 - "Types" of evolution and altruism.

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5. THE EVOLUTION OF HUMAN BEINGS: A BRIEF OVERVIEW [5]

5.1. INTRODUCTION

The evolution of human beings is a topic where knowledge is increasing rapidly, and so ideas and theories may quickly become dated. This article is an overview of some of the understanding of the process at the time writing [6].

The last common ancestor [7] for chimpanzees and humans was 5-7 million years ago (MYA) [8] (Stringer 2008)(figure 5.1).

The development of upright stance, the ability to make tools, and the large brain all occurred after the break from this ancestor (McKie 2008a). Australopithecus anamensis ("ape-man") showed walking on two legs (4.2 MYA). As to why the species moved to two legs is open to debate including to see predators better in the savannah or to carry food.

The first stone tools appeared 2.5 MYA, including cutting meat and cooking it for easier digestion, with Homo habilis. This helped in the brain expansion of about 500 000 YA (McKie 2008a).

The differences between humans and apes can be summarised as (McNamara 1999):

• Longer lifespan and growth periods allowing longer limbs;

• Heterochrony - variation in appearance of different body features producing, for example, ethnic or

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[5] More and updated information at Smithsonian Institution Human Origins Programme (http://anthropology.si.edu/humanorigins/).

[6] May 2009.

[7] Eg: Nakalipithecus nakayamai (Kunimatsu et al 2007).

[8] Because such long periods of time are involved, geological epochs are sometimes used; eg: Miocene (25-5 MYA), Pliocene (5-2 MYA), Pleistocene (2 million - 10 000 YA), and Holocene (current)(Gradstein et al 2009).

"racial" differences in humans;

- Large brain demands energy leading to changes in gut and diet (ie: vegetation not enough, need for complex fats);

- Language.

SPLITS   SPECIES TODAY

(1) PRIMATES   50 MYA

     STREPSIRHINES   →   Ring-tailed lemur

     SIMIANS

(2) SIMIANS 30 MYA

     NEW WORLD MONKEYS   →   Tamarin/Capuchin

(3) SIMIANS 25 MYA

     OLD WORLD MONKEYS   →   Baboons/Macaque

     GREAT APES

(4) GREAT APES   12 MYA

                                →   Orang-utans

(5) GREAT APES   6 MYA

                                →   Gorilla

(6) GREAT APES   4.5 MYA

                                →   Chimpanzees/Bonobos

                                →   Humans

MYA = million years ago

(1) Strepsirhines split away from other primates (called simians)
(2) New World monkeys split from other simians
(3) Old World monkeys split from other simians leaving great apes
(4) Orang-utans split from great apes
(5) Gorillas split from great apes
(6) Great apes divide into chimpanzees (and sub-divide later with bonobos) and humans

(After Byrne 2000)

Figure 5.1 - Key evolutionary splits in primates.

A number of criteria are used to distinguish humans from non-human primates, but recent developments in genetics have shown the loss of certain genes in humans compared to chimpanzees. For example, caspase-12 active in chimpanzees and inactive in humans. This gave the latter an advantage in avoiding severe sepsis (bacteria in the bloodstream) and allowed increased population density (Newton 2006).

5.2. BIPEDALISM

An important question relates to the development of bipedalism (walking on two legs). The forms of locomotion in primates vary from full-time bipedal, knuckle-walking, terrestrial or arboreal quadrupeds, or full-time arboreal climbers (Amaral 2008) [9].

Answers include to free hands, to save energy, to balance on branches, or to give better support for child. In the latter case, primate infants cling to the fur which is limited by the weight of the baby and the strength of the fur (Schultz 2007). So "safety of infant carrying imposes limits on the weight of infants" (Amaral 2008).

The infant-carrying method varies between forest apes in Asia (eg: gibbons) and ground-based African apes (eg: gorillas). In the former, mothers carry the young over one side of the pelvis and not on the back. In gorillas, the babies cling to the front or back, and are aided by support from the mother (Amaral 2008). Richmond et al (2001) felt that "infants (from early hominin biped) probably clung to their mothers' hair.." (quoted in Amaral 2008).

The ability to grip the fur or hair and the slipping risk "imposes clear limits on the maximum body angle attained by heavy ape species carrying infants, representing a hindrance against evolution towards bipedality. This might explain the persistence of knuckle-walking among the great African apes" (Amaral 2008 p288).

Species of Homo did not have the fur for clinging, so the infant had to be carried, and this could have been the "decisive factor" in the evolution of "habitual bipedalism" (Iwamoto 1985). The selective pressure for walking upright would work particularly with females. "The difficulties in locomotion and food gathering for biped females carrying infants may well be at the origin

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[9] Richmond et al (2001) assessed the evolution of the skeleton in relation to different ancestors of bipedalism like arboreal quadruped, terrestrial quadruped, or knuckle-walker.

of the necessity of group cooperation, which could initially have been among females, with males in their usual role of primate group protection" (Amaral 2008 p290).

However, no date has been established for when less body hair appeared in the evolution of hominines [10] (Amaral 2008).

5.3. STAGES IN EVOLUTION OF HUMANS [11]

The stages in the evolution of human beings (or hominids) can be simplified into three time periods (figure 5.2).

i) 6-4 MYA

Three separate species have been found: Sahelthropus tchadensis (unclear if walked upright; Wong 2009) [12], Orroria tugenensis [13], and Ardipithecus ramidus [14] with only the latter having evolutionary connections to later hominids.

ii) 4-2 MYA

Australopithecus anamensis [15] is the key evolutionary development by this time period. Fossils have been found in Kenya for 4.2 MYA. This hominid walked upright and was a woodland inhabitant (McKie 2008c).

Two strands of evolution can be traced from Australopithecus anamensis:

a) Australopithecus line including Australopithecus afarensis, Australopithecus garhi, Australopithecus africanus (figure A5.3), and Paranthropus aiethiopicus (figure A5.4), Paranthropus boisei, Paranthropus robustus.

Australopithecus afarensis has been found in East Africa from 4-3 MYA with the best know fossil being "Lucy". Australopithecus afarensis was bigger than Australopithecus anamensis, and had a vegetarian diet (McKie 2008c).

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[10] The term "hominines" (or hominids) is used to describe "all members of the human group, including humans themselves and their fossil ancestors" (Clegg 2007).

[11] More details at http://www.stanford.edu/~harryg/protected/evolve3.htm.

[12] Details of original fossil discovery in Brunel et al (2002).

[13] See Senut et al (2001) for fossil details.

[14] See Semaw et al (2005) about fossils.

[15] Details of fossils in Meave et al (1995).

Australopithecus africanus has been found 3.5-2.5 MYA in South Africa. Similar to Australopethicus afarensis in body size and vegetarian diet (McKie 2008c).

From this line (Australopithecus afarensis) came Homo habilis (figure A5.5) found in East Africa. The first appearance of stone tools and a brain capacity twice the size of previous hominids, but half that of Homo sapiens (McKie 2008c).

b) Kenyanthropus platyops leading to Homo rudolfensis (figure A5.6).

iii) 2-0 MYA

It is probable that the two lines above in the form of Homo habilis and Homo rudolfensis came together in Homo erectus (Rogers 2008). Homo erectus (figure A5.7) found in East Africa 1.5 MYA probably had no fur, and hunted for meat on the savannah (McKie 2008c).

Next in evolutionary terms came Homo heidelbergensis (found in Germany 500-400 000 YA; McKie 2008c), which in time divided into Homo neanderthalensis (figure A5.8) and Homo sapiens.

Homo neanderthalensis was in Europe from 250 000 to 35 000 YA. They had complex stone tools, buried their dead, and may have used complex speech (McKie 2008c).
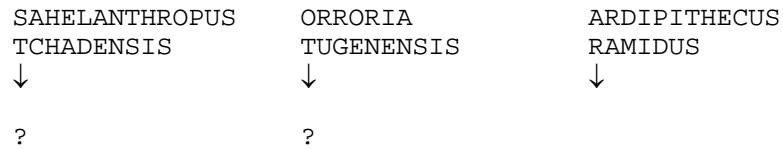
Homo sapiens (figure A5.9) are distinguished by the large brain, symbolic thought, co-operation, and language (McKie 2008c).

There are two other Homo species; at this stage it is unclear about them - Homo antecessor (figure A5.10) and Homo floresiensis (found recently on Flores island, Indonesia)(Knight and Nowak 2004). The latter are very small, and it is disputed as too whether they are a separate species or not (McKie 2008c).

The original ancestor of humans is Homo erectus including the subsequent Homo heidelbergensis. Around 400 000 YA Homo heidelbergensis evolved into Homo neanderthalensis north of the Mediterranean, and into Homo sapiens in Africa (Stringer 2008).

There is a debate over how the process of evolution from Homo erectus occurred. "Multi-regionalists" argue that humans evolved in their own homelands. For example, Neanderthals in Europe evolved into Cro-Magnons. The "out of Africa" theory sees the groups as separate. Neanderthals replaced in Europe, possible violently, by Cro-Magnons migrating from Africa around 45 000 YA (McKie 2008b).

6-4 MYA

SAHELANTHROPUS   ORRORIA   ARDIPITHECUS
TCHADENSIS   TUGENENSIS   RAMIDUS
↓   ↓   ↓

?   ?

4-2 MYA

                                          AUSTRALOPITHECUS
                                          ANAMENSIS
                            ↓   ↓

                      AUSTRALOPITHECUS   KENYANTHROPUS
                      AFARENSIS   PLATYOPS
          ↓   ↓   ↓   ↓

AUSTRALOPITHECUS   ↓   AUSTRALOPITHECUS   ↓
AFFRICANUS   GARHI?
↓   ↓   ↓

PARANTHROPUS   HOMO   HOMO
AETHIOPICUS;   HABILIS   RUDOLFENSIS
PARANTHROPUS
BOISEI;   ↓   ↓
PARANTHROPUS
ROBUSTUS   ↓   ↓

                      →   ?   ←

2-0 MYA

                      HOMO ERECTUS
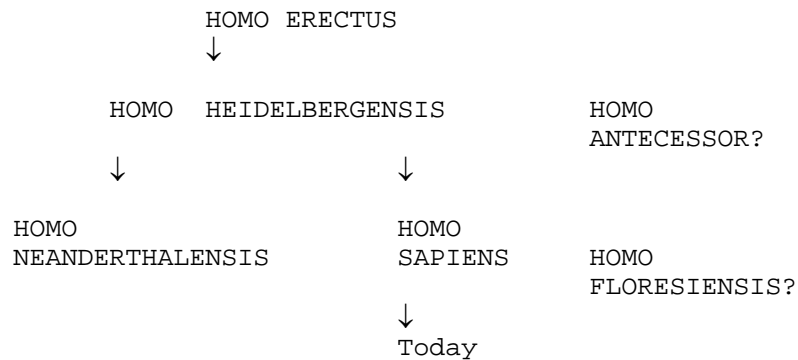   ↓

                HOMO HEIDELBERGENSIS   HOMO
                                                ANTECESSOR?
                ↓   ↓

          HOMO   HOMO
          NEANDERTHALENSIS   SAPIENS   HOMO
                                                      FLORESIENSIS?
                                        ↓
                                        Today

(Source: Rogers 2008)

Figure 5.2 - Basic stages in evolution of human beings.

        A key difference between the different hominids
relates to the brain size (table 5.1).

	HEIGHT (metres)	BRAIN SIZE
Australopithecus	1-1.5	400-500
Homo erectus	1.3-1.5	750-1250
Neanderthal	1.5-1.7	1200-1750
Early modern Homo	1.6-1.85	1200-1700

(Source: Jones et al 1992).

Table 5.1 - Comparison of brain sizes for different hominids.

5.4. CONCLUSIONS

McKie (2008c) summarised the current view: "our evolution was not a business in which one apeman species was replaced every so often by a new, improved version until, eventually, Homo sapiens appeared on the scene. It was a process of experimentation in which our hominid ancestors evolved in several different directions".
Evidence to support this view comes from the fact that aspects of the human body are far from perfect, like blind spot on eye, wisdom teeth, appendix, and DNA replication makes mistakes (Ainsworth and LePage 2007).

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5.6. APPENDIX: IMAGES

(Source: US Federal Government; public domain)

Figure A5.3 - Australopithecus africanus head model.

(Source: Artwork by Walter Voigt - provided by Lee Berger and Brett Hilton-Barber)

Figure A5.4 - Painting of Paranthropus on plains of Africa.

(Source: Guérin Nicolas)

Figure A5.5.- Skull of Homo habilis from museum at
University of Zurich.

(Source: Locutus Borg; public domain

Figure A5.6 - Skull of Homo rudolfensis.

Figure A5.7 - Skull of Homo erectus found in France.

(Source: Public domain)

Figure A5.8 - Skull on Homo neanderthalensis.

Figure A5.9 - Skull of Homo sapien from Germany

(Source: Xvazquez; public domain)

Figure A5.10 - Reconstruction of Homo antecessor skull from museum in Barcelona.